Setting priorities for conservation of the conifer genetic resources of British Columbia

by Alvin D. Yanchuk¹ and Donald T. Lester²

Gene conservation of native conifer species in British Columbia is considered necessary primarily to safeguard the future evolutionary potential of species to climate change, new biotic challenges and for commercial genetic improvement programs. The tactical options include: (i) maintaining existing protected areas, (ii) creating new reserves for *in situ* management, and (iii) *ex situ* collections of various types.

A two-part strategy is presented, with emphasis on technical justifications, for the conservation of conifer tree genetic resources of 23 British Columbia species. Part I is a survey of the frequency of each species in current land reserves in BC. Part II outlines an approach that will aid in setting priorities for additional gene conservation activities for specific species. This process attempts to use information on: (i) levels of *in situ* protection, (ii) the status of each species in current provenance research and breeding programs, and (iii) the relative capabilities for natural regeneration for each species.

Representation of the 23 native conifer species in the current network of protected areas is generally complete. For instance, western hemlock is under little threat, as extensive *ex situ* collections are in field tests; it is well protected in the current reserve network, and it has a great capacity for natural regeneration. At the other extreme, whitebark pine has no *ex situ* collections made to date, needs additional protection in some ecoregions of the province, and generally has poor natural regeneration potential. While implementation of our strategy will be an ongoing process (i.e. updating information from both new and old *in situ* reserves, and setting new priorities among species), several immediate issues have been noted. These include: (i) follow-up work in the area of population sampling for *ex situ* collections, (ii) "ground truthing" of current reserves where data are weak, and (iii) examining the merit of certain populations not located in BC (as they could be as important as those currently protected in BC).

For the future, various broad management questions will need to be resolved, such as: (i) whether existing reserves will perpetuate the various gene pools, and what management will be appropriate for such areas, (ii) the impact of pollen migration from genetically improved production stands on reserve stands, and (iii) the role of commercially improved stands and the breeding populations themselves to meet gene conservation objectives.

Key words: gene conservation, native conifers, British Columbia, tree genetics

Le conservation des gènes des espèces résineuses indigènes de la Colombie-Britannique est considérée comme étant nécessaire principalement pour sauvegarder les possibilités d'évolution dans le futur des espèces face aux changements climatiques, dans le cas de nouveaux défis biotiques et pour utilisation au cours de programmes de d'amélioration génétique. Les options retenues comprennent: (i) le maintien des territoires protégés actuels, (ii) la création de nouvelles réserves pour un aménagement *in situ*, et (iii) des collections *ex situ* de différents types.

Une stratégie en deux parties est présentée, en mettant l'accent sur les justifications techniques, de conservation des ressources génétiques de 23 espèces arborescentes résineuses de Colombie-Britannique. La Partie I comprend un sondage de la fréquence de chacune des espèces au sein des réserves forestières actuelles en C.-B. La Partie II souligne l'approche qui va permettre d'ordonner les priorités des activités additionnelles de conservation génétique pour certaines espèces. Ce processus cherche à utiliser l'information sur: (i) les niveaux de protection *in situ*, (ii) le statut de chacune des espèces par rapport à la recherche actuelle sur la provenance et les programmes d'amélioration, et (iii) les capacités relatives de régénération naturelle de chacune des espèces.

La représentation des 23 espèces résineuses indigènes dans le présent réseau de territoires protégés est pratiquement complétée. À titre d'exemple, la pruche de l'ouest est actuellement peu menacée, puisque de nombreuses collections *ex situ* font l'objet de tests, elle est bien protégée par le réseau actuel de réserves, et elle a une grande capacité de régénération naturelle. À l'opposé, le pin à écorce blanche ne se retrouve pas à ce jour dans des collections *ex situ*, nécessite une protection additionnelle dans certaines écorégions de la province, et est considéré généralement comme ayant un faible potentiel de régénération naturelle. Même si l'implantation de notre stratégie constitue un processus itératif (par ex. la mise à jour de l'information à la fois des récentes et des anciennes réserves *in situ*, et la définition des priorités parmi les espèces), certaines questions doivent être réglées avant toute chose. Parmi ces questions, on retrouve: (i) le suivi des travaux dans le domaine de l'échantillonnage des populations pour des collections *ex situ*, (ii) la vérification sur place des réserves actuelles lorsque les données s'avèrent peu fiables, et (iii) l'étude du mérite de certaines populations hors C.-B. (qui pourraient être autant importantes que celles actuellement protégées en C.-B.).

Diverses questions générales d'aménagement devront être résolues dans l'avenir, à savoir: (i) si les réserves existantes perpétueront les diverses sources génétiques, et quelle forme d'aménagement sera appropriée pour ces réserves, (ii) l'impact de l'apport de pollen en provenance de peuplements à production améliorée sur les peuplements des réserves, et (iii) le rôle des peuplements améliorés à des fins commerciales et des populations améliorées dans le cadre des objectifs de conservation génétique.

Mots clés: conservation génétique, conifères indigènes, Colombie-Britannique, génétique arborescente

Introduction

Needs, justifications and strategies for the conservation of forest tree genetic resources have been discussed at length by many authors (Ledig 1986, 1988; Namkoong 1984; Yang

and Yeh 1992; Zobel 1978). However, very little has been reported on details of development and implementation of conservation theory. This is probably due to the difficulty in setting priorities among species (or populations), as well as determining which gene conservation approaches, i.e., *in situ* versus *ex situ*, or some mixture thereof, are appropriate. While philosophical justifications for this work are relatively easy to develop, quantitative technical justifications are much more difficult

¹Research Branch, British Columbia Forest Service, 31 Bastion Square, Victoria, British Columbia, Canada V8W 3E7.

²Genetic Resource Management Consulting, 1424 North Beach Rd., Salt Spring Island, British Columbia, Canada V8K 1B2.

because each conservation activity must be knowledge, or assumption, based. In addition, clear separations are generally not present for either utilitarian or ecological needs. In other words, does this work have as an end point gene conservation for future genetic improvements by tree breeders, or is it based on our obligation to the integrity and perpetuation of "natural" ecosystems where the species is present? The former may be easier to justify in terms of long-term social economics where relevant discount rates are somewhat certain. The latter is more difficult to defend in a strict economic sense, and, based on genetic principles, may not be needed in many situations. However, it is often very attractive both politically and socially, which can indirectly serve economic ends.

Even from a utilitarian point of view, leaving some wild forest stands to respond to natural evolutionary pressures *in situ*, even though these pressures may be quite subtle (Frankel 1974; Levin and Udovic 1977), seems desirable and may well be the only cost-effective, feasible and long-term approach to gene conservation. *In situ* reserves, with ecological representation as the main goal, can underpin *ex situ* collections made for breeding purposes; conversely *ex situ* collections may be the only security for populations threatened with extinction (Namkoong *et al.* 1988). Therefore, both *in situ* and *ex situ* approaches are likely necessary in a viable gene conservation strategy (Falk 1987; Yang and Yeh 1992), irrespective of a utilitarian or ecological justification.

In BC's gene conservation initiative, emphasis is placed primarily on genetic sampling for future "utilitarian" needs. This approach accommodates the most basic population genetic requirements and serves as an important first step in the development of a gene conservation strategy (Namkoong 1991). Initiatives are also underway for setting aside additional protected areas based on ecological sampling. These new protected areas will greatly expand the province's *in situ* conservation reserves (Province of British Columbia 1993).

Our gene conservation strategy attempts to first examine and identify, by species and region of BC, populations which may require more immediate attention for conservation, and second, for the longer term, to identify and find solutions to management problems for perpetuating the germplasm in the desired form. In this paper, which concentrates on the shorter term concerns, we will present the strategy and its implementation to-date by:

- 1) describing the justification, technical assumptions, and rationale for the tactics recommended for conifer gene conservation in British Columbia;

- 2) discussing the concept of protected areas as reserves for *in situ* gene conservation, present a condensed version of the methodology initially reported in Yanchuk (1995) and Lester and Yanchuk (1996) used to survey genetic resources within these protected areas, and present the results of the survey for 23 native conifers of BC;

- 3) describing the current status of breeding populations and provenance collections (i.e. *ex situ* conservation) and their potential contribution to gene conservation;

- 4) illustrating one quantitative approach to setting priorities for future action.

Some of the longer-term issues that have arisen from this work that need to be resolved in the conservation of forest tree genetic resources are also examined.

Justification and Objectives of Gene Conservation

The development of a clear justification for gene conservation of many BC conifer species is complicated by two factors. First, many commercially important conifers have a wide geographical distribution and are quite common in many ecosystems. For example, white spruce (*Picea glauca* Monch. Voss) occurs from BC to Newfoundland. Moreover, many of BC's tree species are capable of substantial reproduction and re-colonization in highly disturbed ecosystems. Except in special situations (such as outlier populations), these species (or populations) may require no, or little attention. Decisions to do nothing, however, can be viewed as part of a gene conservation strategy.

Second, for species undergoing genetic improvement, breeding populations contain a large number of genotypes which carry many of the useful alleles a breeder may require. Population sizes as small as 120 individuals have a probability greater than 90% of sampling any allele occurring at a frequency of 5% (Gregorius 1980). While this type of genetic sampling theory is more relevant to oligogenic traits, the case for large sample sizes for traits affected by polygene systems is likely weaker. Even with population sizes that are relatively small (e.g. approximately 40), substantial genetic response has been observed over many generations (Madalena and Robertson 1975) as new variants arise through mutation (Hill 1982) and from the conversion of non-additive variance to additive genetic variance (Bryant *et al.* 1986; Goodnight 1988). Therefore, genetic variation available in most large breeding populations will likely be present to meet a wide array of traits for a range of desirable characteristics that may be required in future. This will be particularly true for improvement programs that have multiple-trait or multiple-environment breeding objectives (Eriksson *et al.* 1993).

Why, then, are we concerned about gene conservation in forest trees? The primary justification is as follows: relatively few genotypes in current breeding or wild populations are expected to have low-frequency alleles. If low-frequency alleles become of interest for future breeding objectives, or for the survival of a wild population, the possibility of relatedness among selected or surviving genotypes may not allow effective use of these low-frequency genes due to excessive inbreeding build-up, when matings occur to increase the allele frequencies (in both domestic or wild populations). Therefore, it is desirable to raise the probability that rare genes will be available in enough unrelated genotypes in either wild or breeding populations.

With continued improvements in biotechnology, primarily with the opportunities provided by transgenics, the above justification could become very weak, as low-frequency alleles could be moved into the appropriate genetic backgrounds. However, at this time, we cannot see biotechnology being a dependable substitute for a network of solidly based genetic resources.

Technical Assumptions and Rationale for Gene Conservation Activities

The above justification provides the guiding principle for development and implementation of a gene conservation strategy for conifer tree species in BC. However, a technical rationale is needed to formulate specific activities that allow

us to meet the stated objectives. There are five important technical points to consider.

1) We assumed that genetic differentiation is mostly the consequence of natural selection and has tracked geographic, climatic and ecological variation. While there are departures from this assumption, either in the form of differences among species in fitness from genecological differentiation or in recolonization from different refugia (i.e. genetic drift), it provides a reasonable conservation framework in the absence of other information. Current knowledge of the patterns of genetic variation associated with geography and the distribution of genetic variation among and within populations was used. This kind of information originates from genecological studies (Rehfeldt 1979, 1984; Ying *et al.* 1985; Ying 1995) and from allozyme studies. Therefore, we feel our approach is very conservative in that we will likely over-sample from what is statistically "optimal." Even when substantial research has been done on a particular species, the assumption is still valid because marginal or outlier populations may not be adequately represented in such studies.

2) "Populations" are viewed as the basic unit for gene conservation, even though we are specifically interested in alleles. The assumption is that enough individuals can be "sampled" to capture alleles at roughly their current frequencies in the population.

3) Populations at the edge of a species' range, particularly geographic outliers, are priority candidates for conservation activities as they are more likely to differ genetically. In addition, they may be more vulnerable than core populations to environmental change due to lower levels of genetic variation resulting from unique environmental selection pressures, reduced gene flow via isolation, or genetic drift (i.e. descendants established from a few progenitors). While the genetic reasons for the evolution of "uniqueness" in outlier populations may be currently unknown, substantial genetic gains can be realized from these populations (e.g. California outlier populations of Sitka spruce grown in BC exhibit significantly higher growth potential: J.N. King, BC Forest Service, unpublished data). Another example in forest trees is the Guadalupe and Cedros Island populations of *Pinus radiata*. These populations have shown large differences in disease resistance (Old *et al.* 1986) and other characteristics (Moran *et al.* 1988). Our assumption about the value of marginal populations may be overly conservative as Brown and Briggs (1991) have pointed out that until evidence on the comparative adaptability of marginal populations is available, no bias should operate for or against marginality *per se*.

4) The preservation of "co-adapted gene complexes" is often mentioned as an important objective in gene conservation. Co-adapted gene complexes would arise from selection favouring "sets of genes" in relation to specific environments. This means that for either *in situ* or *ex situ* gene conservation, new gene combinations must be continually available to respond to new selection pressures. For *in situ* conservation, a changing climate will present different selection pressures which may be accommodated only if trees are reproducing through sexual recombination. *In situ* reserves without natural regenera-

tion would thus be analogous to *ex situ* seed storage, or gene archive plantations, because there are no new sets of genes on which selection can act. For *ex situ* methods, a comprehensive tree breeding program offers a continuing flow of genetic recombination (and variation) which can be tested in multiple environments. Field testing in relevant environments should assure that co-adapted gene complexes for survival and growth will be maintained.

5) Some populations in seemingly "central" areas of the species distribution, may occupy peripheral environments and may have evolved very different gene frequencies. While this may be rare, there are important examples such as Sitka spruce resistance to the terminal weevil *Pissodes strobi* in ecologically peripheral coastal environments (Ying 1991). Unfortunately, the location of these unique selection pressure areas may be difficult to predict. This is where an *in situ* conservation strategy based on ecological considerations may assist greatly.

Tactical Options: Three Gene Conservation "Vehicles"

Gene conservation must be done using practical and effective methods which are integrated with other activities and uses of the land. The following describes three gene conservation "vehicles" that are currently or potentially available in BC.

1) Current and Prospective Unmanaged Reserves

The use of existing protected areas for gene conservation offers large, relatively undisturbed tracts of land where human intervention is restricted by legislation. In BC, reasonable efforts are made to keep protected areas in their current "natural" state, but fire management policies in parks sometimes allow wildfires to burn which may adversely affect their utility in this regard.

Current protected areas are attractive for long-term conservation; but three problems are associated with these. First, these reserves are not managed to perpetuate the current forest composition and management to maintain the species and population composition might not even be possible due to natural stand dynamics (i.e. successional replacement). Second, these reserves are typically natural stands where it is difficult to observe genetic variation, as the requisite environmental challenge (e.g. climate or pests) may not be present to resolve certain genetic variations of interest. Third, loss by political, biotic or abiotic causes is possible. Despite these shortcomings, current reserves will be subject to local evolutionary pressures and may maintain large numbers of genotypes at no additional cost.

2) New Reserves "Managed" for *in situ* Genetic Purposes

Riggs (1982) describes land units which could be managed for Douglas-fir gene conservation in California. His "Genetic Resource Management Units" (GRMU) have, as a primary objective, management for the integrity of the local gene pool. These areas are now being considered in California gene conservation activities (Millar and Libby 1991). Timber harvesting is allowed, and perhaps even required, to accomplish the objective as long as natural regeneration of the target species is possible. Artificial regeneration is also allowed, as long as it uses only "very local" seed.

GRMU's at some point could contribute to the BC gene conservation initiative. They meet the *in situ* requirement for gene conservation while allowing for dynamic management of

the local gene resource. For example, it may be possible to manage the regeneration system so that high-heritability environments are created, making it easier to observe important genetic variations. However, at this point we have not considered them in BC for three reasons. First, the Protected Areas Strategy and our survey of currently protected areas has still to gain acceptance and formalization before we can identify candidate areas for GRMU status. Second, development and implementation of government policy and operating procedures for maintaining a GRMU will require substantial efforts. Third, from the results of the survey presented later, very few GRMU's may actually be required.

3) *Ex situ* Collections and Experimental Plantations

a) General

Ex situ collections can take many forms. As used here, it means any collection or planting of material, not purposely established or held to regenerate itself naturally. Storage of seed with cryopreservation techniques is *ex situ*, as are provenance and progeny tests. In other words, collections in the form of provenance and progeny material are being "held" in forest environments, the same as their seed might be held in cryopreservation. However, both of these forms of *in situ* conservation are still subject to natural selection.

b) Provenance Collections and Tests

Provenance tests typically sample portions of the species distribution that is of interest to provincial reforestation. By design, they expose many diverse genotypes to high-heritability environments, allowing greater resolution of important genetic variation due to minimized local environmental variation.

Unfortunately, many peripheral (marginal) and outlier populations are not sampled in these types of tests. Often their inclusion is not cost effective as the test environments are ecologically unsuitable (e.g. Douglas-fir material from Arizona is poorly adapted to coastal and interior BC). Nevertheless, sampling from a wider range of environments could be desirable in future provenance studies, and justified as part of a gene conservation initiative.

c) Breeding Populations

Tree breeding is the most dynamic and flexible means of gene conservation (Eriksson *et al.* 1993), particularly with the use of multiple breeding populations undergoing different selection pressures (i.e. adaptive and economic traits). Although most tree breeding programs are being structured with multiple populations, it may behoove breeders to invest some of their resources in breeding for increased genetic variation. This would require only slight changes to current strategies, and may be quite relevant in rapidly changing climates. For example, it is clear that Douglas-fir material from Arizona planted in B.C. does not provide a useful timber product, but when it is crossed with local genotypes (and undergoes recombination in subsequent generations) segregation variation could be exposed in useful forms (Namkoong, pers.com.). Also, inter- and intra-species hybridization could provide a source of genetic variation for adaptation to new environments (e.g. Lewontin and Birch 1966).

In summary, different gene conservation vehicles are available in the development of a strategy. It is not feasible or nec-

essary to protect the genetic resources of all species at the same level of intensity. A combination of *in-* and *ex situ* conservation must be developed for each species which considers the reproductive biology, ecological and geographical range, status in existing provenance and breeding programs, and current representation in existing protected areas.

Preliminary Strategy Implementation

As mentioned previously, our strategy attempts to identify populations which require immediate attention for genetic conservation, as well as identify management issues that need to be resolved for adequate perpetuation of important germplasm. The two parts believed to be required to accomplish the objectives stated earlier are:

Part I: Survey of Protected Areas

The first task was to assess the status of each species within the current reserves protected by legislation (i.e. Ecological Reserves, Provincial Parks, National Parks).

1) Ecoregions were used as the first stratification of the province because they represented reasonably good separation both in latitude and longitude as well as gross ecological differences. For each of the province's 32 terrestrial ecoregions (Demarchi 1991) (Fig. 1), Ecological Reserves, Provincial Parks and National Parks greater than 250 ha were listed for each combination of biogeoclimatic (BGC) zone and expected tree species occurrence. (See Tables 1 and 2 for species codes and for biogeoclimatic zone codes.) With the use of BGC zones within each ecoregion a further stratification was attained which largely considers elevation and species communities. Reserves of 250 ha or greater were expected to have a reasonably large number of individuals of the target species to meet conservation concerns. The threshold of 250 ha results in an underestimate of the number of reserves where important protection may exist.

For each combination of species and BGC, the average frequency of the species in that BGC was listed to provide a rough measure of whether the combination was central or peripheral to the ecologic amplitude of the species (e.g. for the Northern Coastal Mountains Ecoregion) (Table 3). Range maps and initial identification of species associations developed by Krajina *et al.* (1982), with subsequent updates (BC Ministry of Forests 1991), were used. Species community lists were available for most Ecological Reserves. Cover maps, as well as some volume data, were generally available for Provincial Parks and National Parks. Volume estimates were provided by the Forest Inventory Report System of the Ministry of Forests (Lester *et al.* 1993).

2) The number of ecological reserves and parks, where a given species might be protected, was tallied by species.

3) Based on knowledge of patterns of genetic variation for many of BC's forest tree species, inventories were screened in each ecoregion by species. The screening task was reduced by sampling ecoregions in three categories. First, were "core" ecoregions where a given species is most frequent and the entire ecoregion is central to the species range in BC. Second, were "peripheral" ecoregions. Peripheral was considered in both the

Fig. 1. Ecoregions of British Columbia, after Demarch (1991).

geographical and biogeoclimatic context of the species distribution (Lester *et al.* 1993). Third, were "outlier" ecoregions, which included populations outside the continuous distribution of the species.

4) Within each category (i.e. ecoregion-BGC zone combination), the Ministry of Forests' Forest Inventory Report System

was surveyed to estimate the "number of stems" present in each of the protected areas. Wood volumes were converted to the "number of trees" based on expected relationships of volume per tree and number of stems per hectare.

5) Areas were identified where additional protection is recommended. Recommendations were based on the number and

Table 1. Species list for conifer species currently under review for gene conservation status in BC

Scientific name	Common name	Code
<i>Abies amabilis</i>	Pacific silver fir	Ba
<i>A. grandis</i>	grand fir	Bg
<i>A. lasiocarpa</i>	subalpine fir	Bl
<i>Chamaecyparis nootkatensis</i>	yellow-cypress	Yc
<i>Juniperus scopulorum</i>	Rocky Mountain juniper	Jr
<i>Larix laricina</i>	tamarack	Lt
<i>L. occidentalis</i>	western larch	Lw
<i>L. lyallii</i>	alpine larch	La
<i>Picea engelmannii</i>	Engelmann spruce	Se
<i>P. glauca</i>	white spruce	Sw
<i>P. mariana</i>	black spruce	Sb
<i>P. sitchensis</i>	Sitka spruce	Ss
<i>P. hybrids</i>	spruce hybrids	Sx
<i>Pinus albicaulis</i>	whitebark pine	Pa
<i>P. banksiana</i>	jack pine	Pb
<i>P. contorta</i>	lodgepole pine	Pl
<i>P. flexilis</i>	limber pine	Pf
<i>P. monticola</i>	western white pine	Pw
<i>P. ponderosa</i>	ponderosa pine	Pp
<i>Pseudotsuga menziesii</i>	Douglas-fir	Fd
<i>Taxus brevifolia</i>	Pacific yew	Tw
<i>Tsuga heterophylla</i>	western hemlock	Hw
<i>Tsuga mertensiana</i>	mountain hemlock	Hm

distribution of reserves and the estimated number of trees in each. Maps of the distribution of protected areas for each species and areas recommended for additional protection are available (Lester and Yanchuk 1996).

Some problems were encountered with the survey. The following are examples of issues that still require resolution:

- 1) As various *Abies* species are identified only as "balsam," a detailed species breakdown for the true firs was not possible.
- 2) The spruce complex (i.e. black, white, engelmann, Sitka and their various hybrids) has not been separable in the basic inventory for many parts of the range of spruce in BC. However, this is not entirely a shortcoming of inventory data. The taxonomy of spruces in BC is complex (e.g. Kiss 1989; Sutton *et al.* 1991), and not yet fully documented.
- 3) Separation of western from mountain hemlock in inventory data is not possible in some parts of BC.

The definition of "adequate protection" has several elements:

- 1) Conservation of alleles is highly dependent of the number of trees in the population. Assuming a random distribution of alleles, alleles with a frequency as low as 0.5% will be conserved if 1200 trees are present. For multiple loci (e.g. 100), a sample of 920 trees will insure a loss of only one allele at one of the loci, where frequency of the rare allele is 0.5% (Namkoong 1988).
- 2) For most species, we considered a "population" in a reserve adequately protected if it is represented by more than 5,000 m³ of wood. A conversion to "number of trees" assumed an average of 0.5 m³ per tree translating into 10,000 trees of "merchantable" size and probably at least 70 years old. This con-

Table 2. List of the 14 biogeoclimatic zones of British Columbia and code abbreviations

Zone Name	Code
Coastal Douglas-fir	CDF
Coastal Western Hemlock	CWH
Mountain Hemlock	MH
Bunchgrass	BG
Ponderosa pine	PP
Interior Douglas-fir	IDF
Interior Cedar – Hemlock	ICH
Montane Spruce	MS
Sub-Boreal Pine – Spruce	SBPS
Sub-Boreal Spruce	SBS
Engelmann Spruce – Subalpine Fir	ESSF
Boreal White and Black Spruce	BWBS
Spruce – Willow – Birch	SWB
Alpine Tundra	AT

version factor will vary substantially by species in different areas of the province. For example, the number of old-growth coastal Douglas-fir trees would be overestimated, and the number of interior spruce trees would be underestimated by this approach (Lester *et al.* 1993). Despite species differences in average volume per tree and volume per hectare, in most cases the number of trees would easily be 5000 which is large enough to cover the recent concerns of Lande (1995) on population sizes needed for long-term population viability.

3) Population sizes estimated by this approach would not have considered trees below merchantable size; therefore, the estimates are conservative. Small trees have the same value as large trees in *in situ* gene conservation, assuming survival probabilities are similar.

4) We also assumed that because the census numbers for individual species will be relatively high in most reserves > 250 ha, genetic drift arising from small numbers or demographic problems (Lande 1989, 1995) will be minimal.

This review confirmed that, for most species, large numbers of trees are protected from harvesting by law. For other species, however, information was either currently unavailable or protection is lacking or inadequate. The details of this survey are presented in Lester *et al.* (1993), and Lester and Yanchuk (1996).

Part II: Setting Priorities for Gene Conservation

While Part I accomplishes an important first step in developing a conservation strategy for the 23 conifer tree species of BC, it alone is not sufficient. At some point, for each species, forest geneticists must reconcile what approach is appropriate for each population of interest. With the information from Part I, we can now use some of the tactics mentioned earlier, one of which is to rely upon the self-sustaining ability of many species in parts of their range. The primary purpose here is to prioritize which populations for the 23 species are in need of some conservation activity.

The following prioritization criteria (posed as questions) were chosen:

- 1) *Is the species "common"?* This was considered relevant, as some species can dominate a particular ecosystem, e.g., west-

Table 3. Example of expected species frequency and protected areas (based on ecological associations) in respective biogeoclimatic zones (BGC) in the Northern Coastal Mountains Ecoregion in each BGC zone. Species codes are in Table 1 and BGC codes are in Table 2. Percentages are the proportion of the ecoregion containing the indicated BGC zone. Expected frequencies are: +++ high, ++ moderate, + low and (+) rare frequency. Protected areas are given by number: PP is provincial park, RA is recreational area, ER is ecological reserve (e.g. ER59 is ecological reserve number 59). Lester et al. (1993) provides the tables for the remaining 31 ecoregions of BC

Biogeoclimatic zones in Northern Coastal Mountain ecoregion						
Tree species	AT (51%)	BWBS (<1%)	MH (16%)	ESSF (5%)	ICH (2%)	CWH (19%)
Ba			+++	(+)		+++
Bl		++ PP689 RA783	++	+++ ER59	++	+ ER59
Se			+	+++ ER59	++	
Sw		+++ PP689 RA783		+ ER59		
Sb		+++ PP689 PP783		+		
Ss			+			+++
Pl ++		+++ PP689 PP783 RA783	+	+++ ER59		+ ER59
Hw			++	+	+++	+++ ER59
Hm			+++	++	+	+
Yc			+++	(+)		++
Cw			+	+	+++	+++
Tw			(+)	(+)	++	++

ern hemlock in the Coastal Western Hemlock BGC system (i.e. CWH, in Table 2). Also, it is assumed that a common species has a reasonably high natural regeneration potential in areas where it is a major component of an ecosystem. Therefore, outlier populations, particularly "small" ones, are the only populations of concern, as larger populations should be relatively self-sufficient.

The "common" status of each species was determined from a table in which the frequency of a particular species in each of 14 biogeoclimatic zones was estimated (BC Ministry of Forests 1991). The number of zones in which each species is found was multiplied by the average frequency in each zone (present but uncommon = 1; common = 2; abundant = 3). With this approach, values ranged from 1 for jack pine to 27 for lodgepole pine. The array of scores was then reversed and divided into three classes: values between 1 and 5 were scored as "3" (now indicating not common), values between 6 and 9 were scored as "2" (now indicating moderately common), and values between 10 and 27 as "1" (now indicating quite common).

2) *Does it have a large range?* The risk of serious loss of genetic material from a species with an extensive range was con-

sidered less than for a species with a small range. Wide-ranging species generally sample a wider spectrum of environments, and are expected to encompass more outlier populations with greater genetic differentiation. This differentiation is also expected to result in a greater capacity to occupy a variety of different environments following disturbance.

Scores were assigned to species as follows based on the percent of the province covered by the species range: < 5% = 3, 5% to 25% = 2, and > 25% = 1 (using range maps of Krajina et al. (1982)).

Populations from outside BC (e.g. coastal Douglas-fir and Sitka spruce from northwestern U.S.) also contain genes of great interest to the province (King and Ying unpublished). However, without national or international cooperation in *in situ* gene conservation being in place, range-wide samples of interest may have to be collected and maintained in BC as the approach presented here is only relevant to populations within the province. *Ex situ* strategies may then make very important contributions towards the range-wide gene conservation of species whose ranges extend beyond provincial borders (e.g. grand fir).

Table 4. Gene conservation problem scores for 23 species based on five criteria for prioritizing need for additional effort. High total scores represent species with high priority. Species are arranged by "reserve status" scores for the extent of the network of legally protected areas. Current high economic value is indicated by an asterisk. Species with "+" are expected to have lower scores due to an unknown status in the "natural regeneration" criteria

SPECIES	Common ¹	Range ²	ENR ³	PT ⁴	BP ⁵	Total
<i>Reserve Status "3"</i>						
Rocky Mountain juniper	2	2	2	3	3	12
Tamarack	3	2	1	3	3	12
Alpine larch	3	3	2	3	3	14
Whitebark pine	3	2	3	3	3	14
Jack pine	3	3	3	3	3	15
Limber pine	3	3	?	3	3	12+
<i>Reserve Status "2"</i>						
Pacific silver fir	2	2	2	2	3	11*
Grand fir	2	3	2	2	3	12
Black spruce	2	1	1	3	3	10
Sitka spruce	3	2	1	1	1	8*
Western white pine	2	2	2	2	1	9
Mountain hemlock	2	2	1	3	3	13
Pacific yew	2	2	?	2	3	9+
<i>Reserve Status "1"</i>						
Subalpine fir	1	1	2	3	3	10*
Yellow cypress	3	2	2	1	1	9*
Western larch	2	3	2	1	1	10*
Engelmann spruce	2	1	2	2	2	9*
White spruce	1	1	2	2	1	7*
Lodgepole pine	1	1	1	1	1	5*
Ponderosa pine	2	3	2	2	3	12*
Douglas-fir	1	1	2	1	1	6*
Western redcedar	1	1	2	1	1	6*
Western hemlock	1	1	1 ^a	2	1	6-7*

¹In maritime climates.

^{1a}"1" is common; "3" is not common

^{2a}"1" indicates a large range; "3" a small range, in B.C.

³Ease of natural regeneration: "1" indicates frequent natural regeneration; "3" indicates infrequent natural regeneration

⁴Provenance testing: "1" indicates species which are in provenance testing programs; "2" indicates species with limited provenance testing; "3" indicates no provenance testing.

⁵Breeding programs: "1" indicates species which are in comprehensive breeding programs; "2" indicates species with a relatively small breeding or selection program; "3" indicates no breeding or selections.

3) *What capacity does the species have for natural regeneration?* Local gene pool perpetuation in the absence of human intervention is dependent upon natural regeneration. However, in small populations on the edges of a species distribution (ecologically or geographically), this capacity could be lowered by many demographic and ecological factors, thereby putting these populations at risk.

Recommended regeneration methods (Weetman and Vyse 1990) were used to derive scores for species for which there is extensive experience with natural and artificial regeneration. Where natural regeneration is the recommended method, a score of "1" was assigned, and where natural regeneration is considered not feasible, species were scored "3" (Table 4). Scores of "2" were assigned to species in the mid-range of natural regeneration potential.

4) *What is the status of species in current reserves?* A species that is well represented in currently protected areas is considered to be at lower risk than a species that is not. Well-represented species were scored as "1"; where additional information about reserve status was needed, scores of "2" were assigned; and where additional information was required, plus where deficiencies in reserve status were noted, a score of "3" was given (Table 4).

5) *Is the species in provenance and breeding programs?* Species under some level of genetic testing are considered better protected than species which are not, other things being considered equal. The number of populations and/or parents represented in tests, and the original distribution of the populations or parents are all important, but variations in program extent will largely be based on species' geographic range and value. For the short term, program size and details of the *ex situ* populations were not considered as important as whether or not they could fall into three broad categories. Also, scores were assigned separately for both provenance-testing programs and breeding programs, as the extent of population sampling usually differs. Extensive "*ex situ* testing" was scored as "1", moderate testing "2" and no testing as "3's" (Table 4), for both provenance and progeny testing.

6) *What is the current or potential economic value of the species?* This again enters into the difficult area of utilitarian and ecological justifications, but clearly a species like Pacific yew required more immediate attention after its rise in profile due to its potential use in cancer treatments (Wheeler and Hehnan 1993), than did Rocky Mountain juniper, for example. Thus potential economic value posed a threat from overharvesting and raised the priority of yew for gene conservation activities.

Many approaches could be used to assemble the above-mentioned criteria into a meaningful priority list. At the very least, the chosen method would point to the species and populations where immediate action is required. These subjective overall "scores" for each of the categories rank the 23 species (Table 4). The range of summed scores indicates how this approach separates species at relatively high risk from those at relatively low risk.

They also support what we expected from a general knowledge of the species assessed to date. Gene conservation for western hemlock in BC presently requires little attention relative to Pacific yew and whitebark pine. Even for Pacific yew, based on our ecological surveys and genetic variation studies (El-Kassaby and Yanchuk 1994), the immediate threat is not great. In the early 1990s, the threat to Pacific yew seemed large, yet within a very short period technological solutions (Wheeler and Hehn 1993), combined with an increased understanding of the distribution and ecology of yew have reduced the immediate gene conservation concerns. Many other concerns might also be over or understated simply because of our relative ignorance of the severity of threats (e.g. blister rust and whitebark pine) (Keane and Arno 1993).

Future Management Issues

With the results of this survey in place, several new questions arise. These newly identified issues that require resolution will vary, but many will be questions of what local actions may be needed. For example, i) follow-up work in the area of population sampling for *ex situ* collections, ii) "ground truthing" of current reserves where data are weak or missing, and iii) examining the merit of certain populations not located in BC, through cooperative gene conservation initiatives or by strategic *ex situ* collections. However, these are local concerns that may be small in comparison to the larger issues that remain. Here we will attempt to identify three of the larger issues that require further attention.

Perpetuation and Management of Existing In-Situ Reserves

Reserves currently accepted as adequate for gene conservation may not keep these features indefinitely. Re-analysis on 10-20 year intervals will be required, and this may be more critical for species with smaller ranges or for those that did not rank low (Table 4). Probably the longevity of existing reserves will be area, species and age-class dependent so monitoring efforts of these areas may be subject to some type of priority setting.

The general expectation of *in situ* reserves is that no or little management will take place and only natural processes will largely determine the evolution of these populations. If, for the most part, this is reasonable (i.e. parks and reserves are managed for recreational purposes and large vegetation management objectives are not considered), then simple monitoring of the state of the tree communities (as they are relevant to the gene conservation needs) may be all that is required. Where losses occur, and a reserve no longer serves its original conservation purpose, then a decision will have to be made regarding the potential for finding a replacement. It is unlikely that any flexible vegetation management options will be available in the system of current reserves (other than by chance or prescribed fire), so in these situations, GRMU's may become the only reasonable replacement gene conservation vehicle.

Effects of Commercial Improved Stands on In-Situ Reserves

A commonly expected threat to *in situ* reserves is that of "genetic contamination" from adjacent commercial plantations, particularly if the plantation estate is very large and in close proximity to the reserve. Pollen flow from the plantations into the reserves is expected to alter gene frequencies in *in-situ* regeneration, from that which would have occurred naturally. Monitoring or re-analysis of *in-situ* reserve status will have to also consider the adjacency and potential pollen contamination from commercial plantations, along with the status of the tree communities of interest within the reserves.

Role of Commercial Improved Stands

Through time, commercial plantation estates with genetically improved material are expected to occupy relatively large areas. The genetic base of these plantations may be relatively small since they should arise from only the best parents in the breeding program. Risk and genetic diversity in commercial plantations is being addressed elsewhere (Bishir and Roberds 1995); but, the sheer numbers of individuals in even-aged well managed conditions could serve as a large reserve for the accumulation of new mutations, if they can be identified. Techniques of molecular genetics might be used to assess the genetic dynamics of large plantations as well as to explain potential problems of co-ancestry. In any event, it may be time to no longer consider the production populations as dead-end populations.

Conclusions

One obvious limitation to this analysis is that it has not considered populations outside of BC. So far, only the provenance research program and a few specific breeding programs that have sampled parents or populations from outside of BC address this concern. It is important for tree breeders to become involved in North American forest tree gene conservation activities, particularly for *in situ* programs, to monitor the safety of relevant wild populations, or to make strategic *ex situ* collections. Also, the logic and framework of this approach could be considered in national or international gene conservation activities.

Rankings (Table 4) are a first approximation of what may be the current priorities for conservation, but it is expected that these will change as new information is acquired. Our challenge is to continue to gather this information, and to implement the necessary tactics to ensure adequate conservation of BC's conifer genetic resources. In conclusion, this survey provides a fundamental need in the development of an overall strategy for managing the conifer genetic resource in BC. Some important problems of future management of genetic resources remain to be resolved. But whatever the appropriate solutions may prove to be this survey and analysis appear to be a necessary beginning.

Acknowledgements

The authors would like to thank E.M. Campbell for the tremendous efforts in obtaining data from the inventories of parks and reserves in BC, and for putting together the results of the survey of protected areas. We are also grateful for the reviews provided by Cheng Ying and Barry Jaquish on previous versions of this manuscript, to Jack Woods and Fiona Chandler for comments on a later version, to Rowland Burdon for his considerable comments on logic and wording of particular sec-

tions, and to Jim Pojar for reviewing the data on species occurrence in protected areas of the province.

References

- BC Ministry of Forests. 1991. Ecosystems of British Columbia. D. Meidinger and J. Pojar (Eds.). Victoria, BC.
- Bishir, J. and J. Roberds. 1995. Analysis of failure time in clonally propagated plant populations. *Math. Biosci.* 125: 109–125.
- Brown, A.H.D. and J.D. Briggs. 1991. Sampling strategies for genetic variation in *ex situ* collections of endangered plant species. pp. 99–122. *In* Genetics and conservation of rare plants. D.A. Falk and K.E. Holsinger (Eds.). Oxford University Press, New York, NY.
- Bryant, E.H., S.A. McCommas and L.M. Combs. 1986. The effect of an experimental bottleneck upon quantitative genetic variation in the housefly. *Genet.* 114: 1191–1211.
- Demarchi, D.A. 1991. Ecoregions of British Columbia. 2nd. Edition. BC Environment, Wildlife Branch, Victoria, BC.
- El-Kassaby, Y. and A.D. Yanchuk. 1994. Genetic diversity, differentiation and inbreeding in Pacific yew from British Columbia. *J. Hered.* 85: 112–117.
- Eriksson, G., G. Namkoong and J.H. Roberds. 1993. Dynamic gene conservation for uncertain futures. *For. Ecol. Manage.* 62: 15–37.
- Falk, D.A. 1987. Integrated conservation strategies for endangered plants. *Nat. Areas J.* 7: 118–123.
- Frankel, O.H. 1974. Genetic conservation: our evolutionary responsibility. *Genet.* 78: 53–65.
- Gregorius, H.R. 1980. The probability of losing an allele when diploid genotypes are sampled. *Biom.* 36: 643–652.
- Goodnight, C.J. 1988. Epistasis and the effect of founder events on the additive genetic variance. *Evolution* 42: 441–454.
- Hill, W.G. 1982. Predictions of response to artificial selection from new mutations. *Genet. Res., Camb.* 40: 255–278.
- Keane, R.E. and S.F. Arno. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. *West. J. Appl. For.* 8: 44–47.
- Kiss, G.K. 1989. Englemann $\times$ Sitka spruce hybrids in central British Columbia. *Can. J. For. Res.* 19: 1190–1193.
- Krajina, V.J., K. Klinka and J. Worrall. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Faculty of Forestry, University of British Columbia, Vancouver, BC.
- Lande, R. 1989. Genetics and demography in conservation biology. *Science* 241: 1455–1460.
- Lande, R. 1995. Mutation and conservation. *Conserv. Biol.* 9: 872–791.
- Ledig, F.T. 1986. Conservation strategies for forest gene resources. *For. Ecol. Manage.* 14: 77–90.
- Ledig, F.T. 1988. The conservation of diversity in forest trees. *BioSci.* 38: 431–439.
- Lester, D.T., E.M. Campbell and A.D. Yanchuk. 1993. A gene conservation strategy for BC conifers. Part I. A survey of protected areas for the maintenance of genetic resources of conifers of British Columbia. BC Ministry of Forests, Research Report. Unpublished Internal Report.
- Lester, D.T. and A.D. Yanchuk. 1996. A survey of the protected status of conifers in British Columbia: *in situ* gene conservation. BC Ministry of Forests, Research Report No.04, Victoria, BC.
- Levin, S.A. and J.D. Udovic. 1977. A mathematical model of coevolving populations. *Am. Nat.* 111: 657–675.
- Lewontin, R.C. and L.C. Birch. 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution* 20: 315–336.
- Madelena, F.E. and A. Robertson. 1975. Population structure in artificial selection: studies with *Drosophila melanogaster*. *Genet. Res., Camb.* 25: 113–126.
- Millar, C.I. and W.J. Libby. 1991. Strategies for conserving clinal, ecotypic and disjunct population diversity in widespread species. pp. 149–170. *In* Genetics and conservation of rare plants. D.A. Falk and K.E. Holsinger (Eds.). Oxford University Press, New York, NY.
- Moran, G.F., J.C. Bell and K.G. Eldridge. 1988. The genetic structure and the conservation of the five natural populations of *Pinus radiata*. *Can. J. For. Res.* 18: 506–514.
- Namkoong, G. 1984. Strategies for gene conservation in forest tree breeding. *In*: Yeatman, Kafton and Wilks (Eds.). Plant gene resources: a conservation imperative. AAAS Selected Symp. 87, Westview Press, Boulder, CO. pp. 79–89.
- Namkoong, G., H.C. Kang and J.S. Brouard. 1988. Tree breeding: principles and strategies. Monog. Theor. Appl. Genet. No. 11. Springer-Verlag, New York, NY.
- Namkoong, G. 1988. Sampling for germplasm collections. *Hortscience* 23: 79–81.
- Namkoong, G. 1991. Biodiversity — issues in genetics, forestry and ethics. *For. Chron.* 68: 438–443.
- Old, K.M., Libby, W.T., Russell, J.H. and K.G. Eldridge. 1986. Genetic variability in susceptibility of *Pinus radiata* to western gall rust. *Silv. Genet.* 35: 145–149.
- Province of British Columbia. 1993. A protected areas strategy for British Columbia. Queens Printer #96172, Victoria, BC.
- Rehfeldt, G.E. 1979. Ecotypic differentiation in populations of *Pinus monticola* in north Idaho — myth or reality. *Am. Nat.* 114: 627–636.
- Rehfeldt, G.E. 1984. Microevolution of conifers in the northern Rocky Mountains: A view from common gardens. *In*: Proc. 8th North Amer. For. Biol. Wrkshp. R.M. Lanner (Ed.). Utah State University, Logan, UT. pp. 32–46.
- Riggs, L.R. 1982. Douglas-fir genetic resources: An assessment and plan for California. California gene resource program, Sacramento, CA.
- Sutton, B.C.S., D.J. Flanagan, R. Gawley, C.H. Newton, D. Lester and Y.A. El-Kassaby. 1991. Inheritance of chloroplast and mitochondrial DNA in *Picea* and composition of hybrids from introgression zones. *Theor. Appl. Genet.* 82: 242–248.
- Weetman, G. and A. Vyse. 1990. Natural regeneration. pp. 118–129. *In*: Regenerating British Columbia's Forests. D.P. Lavender *et al.* (Eds.). University of British Columbia Press, Vancouver, BC.
- Wheeler, N.C. and M.T. Hehn. 1993. Taxol: a study in technology commercialization. *J. For.* 91: 15–18.
- Yanchuk, A.D. 1995. A gene conservation strategy for BC conifers: a summary of current approaches. Petawawa National Forestry Institute, Information Report PI-X-119. pp. 3–14.
- Yang, R.C. and F.C. Yeh. 1992. Genetic consequences of *in situ* and *ex situ* conservation of forest trees. *For. Chron.* 68: 720–729.
- Ying, C.C., K. Illingworth and M.R. Carlson. 1985. Geographic variation in lodgepole pine and its implications for tree improvement in British Columbia. Proc. Symp. on Lodgepole Pine — the Species and its Management. Co-op. Ext. Wash. State Univ., Pullman, WA. pp. 45–53.
- Ying, C.C. 1991. Genetic resistance to the white pine weevil in Sitka spruce. Res. Note. No. 106. BC Ministry of Forests, Victoria, BC.
- Ying, C.C. 1995. Long-term provenance tests as source information for gene conservation of forest species. Petawawa National Forestry Institute, Petawawa, ON. Information Report PI-X-119. pp. 15–20.
- Zobel, B. 1978. Gene conservation — as viewed by a forest tree breeder. *For. Ecol. Manage.* 1: 339–344.